



## A morphological search for *Lachnagrostis* among the South African *Agrostis* and *Polypogon* (Poaceae)

Austin J. Brown

Royal Botanic Gardens Victoria, Birdwood Avenue, Private Bag 2000, South Yarra 3141, Victoria, Australia;  
e-mail: austinjamesbrown@gmail.com

### Introduction

The grass subtribe Agrostidinae Fr. of tribe Poeae R.Br. contains 17 genera according to Soreng et al. (2007), of which *Lachnagrostis* Trin., *Agrostis* L. and *Polypogon* Desf. are three. Delimitation of these genera has often been problematic and no less so than in South Africa. Despite a number of recent studies, the phylogeny of the Poeae is still only partly resolved (Soreng et al. 2007; Quintanar et al. 2007; Schneider et al. 2009; Saarela et al. 2010). In addition, these phylogenies have not included adequate representation of the complete Agrostidinae. Until such work is undertaken, morphological assessments have a role to play in segregating species into circumscribed genera.

The genus *Lachnagrostis* includes 31 species endemic to Australia (Jacobs & Brown 2009) and New Zealand (Edgar & Connor 2000). Although first described by Trinius (1820), based on six Australasian taxa, *Lachnagrostis* has only been recognised in New Zealand and Australia in the last 40 years. Bentham (1878) in Australia and Cheeseman (1906) in New Zealand regarded currently recognised *Lachnagrostis* taxa as species of *Deyeuxia* P.Beauv. In New Zealand, Zotov (1965) recognised *Lachnagrostis* as distinct from *Deyeuxia* but only transferred some of the current taxa. It remained for Edgar (1995) to transfer the remainder, as well as to describe new species and subspecies for the New Zealand flora. In

### Abstract

Three South African *Agrostis* L. taxa are transferred to *Lochnogrostis* Trin., as *L. eriantho* (Hack.) A.J.Br., *L. huttonioe* (Hack.) A.J.Br. and *L. polypogonoides* (Stapf) A.J.Br. on the basis of high palea to lemma length ratios and a lack of a trichodium net pattern on the lemma epidermis. However, the lemmas of *L. barbuligera* var. *borbuligera* and *A. barbuligera* var. *longipilosa* Gooss. & Papendorff have a trichodium net and do not belong in *Lachnagrostis*. Instead, they are morphologically similar to a group of montane tropical African *Agrostis*, which includes *A. killimondscharico* Mez. and *A. monnii* (Hook.f.) Stapf. Previous transfers of *A. griquensis* Stapf and *A. viridis* Gouan to *Polypogon* are confirmed as appropriate, as they lack a trichodium net but, unlike *Agrostis* and *Lochnogrostis*, their spikelets disarticulate below the glumes.

**Key words:** taxonomy, Agrostidinae, lemma epidermis, trichodium net

Australia, Mueller (1888) combined *Deyeuxia* and *Agrostis* under *Agrostis*, but Vickery (1940) recognised both genera, regarding current *Lachnagrostis* taxa as species of *Agrostis*. It was to be 60 years until *Lochnagrostis* was segregated from *Agrostis* by Jacobs (2001). Twenty years earlier, Rúgolo de Agrasar (1982) had ascribed the Australasian Common Blown-grass, naturalised in South America, to *L. filiformis* (G.Forst.) Trin. Rúgolo de Agrasar & Molina (2002) transferred the Ecuadorian endemic *A. sodiroono* Hack. to *L. sodiroono* (Hack.) Rúgolo & A.M.Molina, based on its similarities in gross morphological and lemma epidermis features to *L. filiformis*. They also made new combinations for the South African *A. barbuligera* Stapf, *A. lochnantho* Nees and *A. schlechteri* Rendle as *L. borbuligera* (Stapf) Rúgolo & A.M.Molina, *L. lochnantha* (Nees) Rúgolo & A.M.Molina and *L. schlechteri* (Rendle) Rúgolo & A.M.Molina, respectively, but without discussion of their morphological affinity to other *Lochnagrostis*. These new combinations do not appear to have been accepted in South Africa as yet (POSA 2009).

The genus *Agrostis* has 200+ species with representatives in Europe, Asia, North America, South America, Australasia and Africa. These grasses are largely confined to temperate regions and tropical mountains but some species do occur on subantarctic islands. Subdivision of this large and diverse genus has been attempted by a number of authors, as amply described by Björkman (1960). On the basis of a few distinct characters, other *Agrostis* taxa, apart from *Lachnagrostis*, have been segregated into small regional genera, e.g. *Podogrostis* (Griseb.) Scribn. & Merr. (1910) in the Americas, *Neoschischkinia* Tzvelev (1968) in southern Europe and North Africa, *Keniochloa* Melderis (1956) in East Africa and *Zingero* P.A.Smirn. (1946) for the monotypic *Z. biebersteiniana* (Claus) P.A.Smirn. of the Caucasus Mountains. However, diffuse morphological character boundaries and/or intergeneric hybridisation between members of the subtribe Agrostidinae (e.g. *Colomogrostis* Adans. and *Deyeuxia* Clarion ex P.Beauv., *Calomagrostis* and *Ammophila* Host, *Agrostis* and *Polypogon* Desf.) have been the source of uncertainty in the placement of some taxa.

The genus *Polypogon* has approximately 20 species, with the majority being endemic to Mediterranean Europe and south-west Asia and a few species native to the Americas, Africa and Australia. The southern

European *Polypogon monspeliensis* Desf. has become a weedy introduction throughout the world. Aside from some confusion surrounding the nomenclature of *Agrostis* × *Polypogon* hybrids, the taxonomic treatment of *Polypogon* taxa outside Eurasia has been problematic. In Africa, some species have been historically placed in *Agrostis*, a number of South American taxa have been transferred from *Polypogon* to *Choetotropis* Kunth on the basis of intermediate character states between typical *Agrostis* and *Polypogon* (Björkman 1960) and the generic placement of the Australian species, *P. tenellus* R.Br. has been questioned (Weiller et al. 2009).

Stapf (1900) recognised eight *Agrostis* and two *Polypogon* species for South Africa: the native *A. borbuligera* Stapf, *A. bergiana* Trin., *A. griquensis* Stapf, *A. lochnantho* Nees, *A. natalensis* Stapf, *A. polypogonoides* Stapf, *A. schlechteri* Rendle (in the addendum) and *P. tenuis* Brogn. and the exotic *A. verticillata* Vill. and *P. monspeliensis* (Table 1). Soon after, Hackel (1904) described *A. eriontha* Hack. from the Transvaal and Stapf (1908) described *A. suavis* Stapf from Natal. Bews (1918) listed the same *Agrostis* and *Polypogon* species Stapf (1900) had accepted and only added *A. suavis*. Wood (1908) had earlier reported that Dr. Stapf considered *A. suavis* to be closely related to *A. eriantha*, differing only in its divaricate, effuse panicle compared to the narrow contracted panicle of the latter. If accepted as the same taxon, the name *A. eriontha*, as the earlier name, should have priority.

Goossens and Papendorf (1945) listed ten *Agrostis* species for South Africa, with the inclusion of *A. huttoniae* (Hack.) C.E.Hubb. ex Gooss. & Papendorf. The name *A. semiverticillata* (Forssk.) C.Chr. replaced *A. verticillata* Vill. and the name *A. eriantha* Hack. replaced *A. suavis* Stapf. They also described three new varieties: *A. borbuligera* var. *longipiloso* Gooss. & Papendorf, *A. eriontha* var. *planifolia* Gooss. & Papendorf and *A. lochnantha* var. *globro* Gooss. & Papendorf.

Goossens and Papendorf (1945) separated *A. huttoniae* from *A. lochnantho* on the basis that the former had a long, hairy callus and a distinct rachilla extension. Launert (1971) considered *A. huttoniae* to be synonymous with *A. lochnantho* and although Ross (1972) added *A. huttoniae* to the *Flora of Natal*, he was concerned that it lacked satisfactory characters to differentiate it from *A. lochnantho*.

**Table 1.** *Agrostis* and *Polypogon* taxa in South African treatments (accepted taxon names in bold)

Stapf (1900)	Goossens & Papendorf (1945) <sup>1</sup>	Gibbs Russell et al. (1990)
<i>P. adscensionis</i> Trin. (syn. <i>P. tenuis</i> Brongn.)		
<i>A. aristulifera</i> Rendle (syn. <i>A. bergiana</i> Trin.)		
<i>A. alba</i> var. <i>schimperiana</i> Engl. (syn. <i>A. verticillata</i> Vill.)		
	<i>A. albimontana</i> Mez (syn. <i>A. bergiana</i> Trin.)	
		* <i>A. avenacea</i> J.F.Gmel.
<i>A. barbuligera</i> Stapf	<i>A. barbuligera</i> Stapf	<i>A. barbuligera</i> Stapf
	<i>A. barbuligera</i> var. <i>longipilosa</i> Gooss. & Papendorf	<i>A. barbuligera</i> var. <i>longipilosa</i> Gooss. & Papendorf
<i>A. bergiana</i> Trin.	<i>A. bergiana</i> Trin.	<i>A. bergiana</i> Trin.
<i>A. bergiana</i> var. <i>laeviscula</i> Stapf	<i>A. bergiana</i> var. <i>laeviscula</i> Stapf (syn. <i>A. bergiana</i> Trin.)	<i>A. bergiana</i> var. <i>laeviscula</i> Stapf
	<i>A. bergiana</i> var. <i>mutica</i> Hack. (syn. <i>A. bergiana</i> Trin.)	
<i>A. capensis</i> Steud. (syn. <i>A. bergiana</i> Trin.)		
	<i>A. continuata</i> Stapf [unable to verify diff. to <i>A. natalensis</i> ]	<i>A. continuata</i> Stapf
<i>A. dregeana</i> Steud. (syn. <i>A. lachnontho</i> Nees)		
<i>A. ecklonis</i> Trin. (syn. <i>A. bergiana</i> Trin.)		
	<i>A. eriantha</i> Hack.	<i>A. eriantha</i> Hack.
	<i>A. eriantha</i> var. <i>planifolia</i> Gooss. & Papendorf	<i>A. eriantha</i> var. <i>planifolia</i> Gooss. & Papendorf
		* <i>A. gigantea</i> Roth
	<i>A. huttoniae</i> (Hack.) C.E.Hubb. ex Gooss. & Papendorf	<i>A. huttoniae</i> (Hack.) C.E.Hubb. ex Gooss. & Papendorf (syn. <i>A. lachnantha</i> Nees)
<i>A. griquensis</i> Stapf	<i>A. griquensis</i> Stapf	<i>P. griquensis</i> (Stapf) Gibbs Russell & Fish
<i>A. gymnostyla</i> Steud. (syn. <i>Cinna mexicana</i> Beauv.)		
<i>A. lachnantha</i> Nees	<i>A. lachnantha</i> Nees	<i>A. lachnantha</i> Nees
	<i>A. lachnantha</i> var. <i>glabra</i> Gooss. & Papendorf	<i>A. lachnantha</i> var. <i>glabra</i> Gooss. & Papendorf (syn. <i>A. lachnantha</i> Nees)
		<i>P. minutiflorus</i> Pilg. (syn. <i>P. griquensis</i> (Stapf) Gibbs Russell & Fish)
* <i>P. monspeliensis</i> Desf.		* <i>P. monspeliensis</i> Desf.
<i>P. monspeliensis</i> var. <i>capensis</i> Steud. (syn. <i>P. monspeliensis</i> Desf.)		
		* <i>A. montevidensis</i> Spreng. ex Nees
<i>A. natalensis</i> Stapf	<i>A. natalensis</i> Stapf	<i>A. natalensis</i> Stapf (syn. <i>A. continuata</i> Stapf)
<i>A. neesii</i> Trin. (syn. <i>A. lachnantha</i> Nees)		
<i>A. panicea</i> (L.) Aiton (syn. <i>P. monspeliensis</i> Desf.)		
	<i>A. papposa</i> Mez (syn. <i>A. huttoniae</i> (Hack.) C.E.Hubb. ex Gooss. & Papendorf)	
	<i>A. phalaroides</i> Hack. (syn. <i>A. natalensis</i> Stapf)	
<i>A. polypogonoides</i> Stapf	<i>A. polypogonoides</i> Stapf	<i>A. polypogonoides</i> Stapf
<i>P. polysetus</i> Steud. (syn. <i>P. monspeliensis</i> Desf.)		
<i>A. schlechteri</i> Rendle	<i>A. schlechteri</i> Rendle	<i>A. schlechteri</i> Rendle
	* <i>A. semiverticillata</i> (Forssk.) C.Chr.	* <i>A. semiverticillata</i> (Forssk.) C.Chr. (syn. <i>P. viridis</i> (Gouan.) Breistr.)
		* <i>P. semiverticillatus</i> (Forssk.) Hyl. (syn. <i>P. viridis</i> (Gouan.) Breistr.)
<i>A. stolonifera</i> Thunb. (syn. <i>A. bergiana</i> Trin.)		
<i>P. strictus</i> Nees (syn. <i>P. tenuis</i> Brongn.)		<i>P. strictus</i> Nees
	<i>A. suavis</i> Stapf (syn. <i>A. eriantha</i> Hack.)	
<i>P. tenuis</i> Brongn.		



Table 1 cont. *Agrostis* and *Polypogon* taxa in South African treatments (accepted taxon names in bold)

Stapf (1900)	Goossens & Papendorf (1945) <sup>1</sup>	Gibbs Russell et al. (1990)
	<i>A. subulifolia</i> Stapf (syn. <i>A. bergiana</i> Trin.)	<i>A. subulifolia</i> Stapf
<i>*A. verticillata</i> Vill.	<i>*A. verticillata</i> Vill. (syn. <i>A. semiverticillata</i> (Forssk.) C.Ch.)	
<i>A. vestita</i> Hochst. ex A. Rich. (syn. <i>A. lachnantha</i> Nees)		
		<i>*P. viridis</i> (Gouan.) Breistr.
<sup>*</sup> exotic taxon		
<sup>1</sup> deals only with <i>Agrostis</i> taxa		

Ross (1972) included *A. subulifolia* Stapf and *A. bergiana* var. *laeviscula* Stapf to the plants of Natal, as did Gibbs Russell et al. (1990) to the grasses of southern Africa (Table 1), despite Goossens and Papendorf (1945) having previously considered *A. subulifolia* to be synonymous with *A. bergiana* Trin. and not recognising any varieties of *A. bergiana* (Table 1).

Gibbs Russell et al. (1990) added the Australasian *A. avenacea* J.F.Gmel. (syn. *Lachnagrostis filiformis* (G.Forst.) Trin.), the European and temperate Asian *A. gigantea* Roth. and the South American *A. montevidensis* Spreng. ex Nees. to the list of southern African *Agrostis* and recognised *A. continuata* Stapf for South Africa, treating *A. natalensis* in synonymy. They transferred *A. griquensis* Stapf to *Polypogon* as *P. griquensis* (Stapf) Gibbs Russ. & Fish (not validly so until Fish (2006)) and treated *A. semiverticillata* (Forssk.) C.Ch. as *Polypogon viridis* (Gouan.) Breistr. (Table 1). Gibbs Russell et al. (1990) also listed *P. strictus* Nees but not *P. tenuis*. Although Stapf (1900) treated *P. tenuis* from Ascension Island (mid South Atlantic Ocean) in synonymy with *P. strictus*, as has Clayton et al. (2002 onwards) (*P. tenuis* having priority as the earlier name), Goldblatt and Manning (2000) and Raimondo et al. (2009) did not do so.

To add to the transfers from *Agrostis* to *Polypogon*, Clayton et al. (2006 onwards) invalidly treat *A. polypogonoides* Stapf as *P. polypogonoides* (Stapf) Forsan: their attribution of the ‘author’ Forsan being in error – this merely meaning ‘perhaps’ in Latin.

As part of a wider study of *Lachnagrostis* by Brown (2013), the opportunity to examine herbarium specimens of South African collections raised the possibility that taxa accepted in that country as *Agrostis* or *Polypogon* may better conform to Australasian concepts of *Lachnagrostis*. This paper examines the

morphological evidence for the generic placement of all the native and introduced South African *Agrostis* and *Polypogon* into *Lachnagrostis*, *Agrostis* or *Polypogon*.

Materials and methods

Morphological characters that are considered critical in establishing generic concepts of *Agrostis*, *Lachnagrostis* and *Polypogon* were compiled from the literature for South African and Australasian taxa (Table 2). The values of these characters were derived from the original descriptions of the taxa, unless such were not provided, wherein they were supplemented from later descriptions. Additional descriptions of Eurasian and North American taxa were also consulted to provide a wider context for these genera. Owing to the varied treatment of *Agrostis* and *Polypogon* in Central and South America (e.g. sometimes as *Bromidium* Nees & Meyen and *Chaetotropis*, respectively), these taxa were mostly excluded from consideration in the current study. Likewise, in order to simplify the study, attention is not given to East, Central or West African *Agrostis* and *Polypogon*, although it is recognised that an Africa-wide study of these taxa would be beneficial in due course.

Forty-nine herbarium specimens of South African *Agrostis*, *Polypogon* and *Lachnagrostis* taxa housed at MEL and on loan from PRE (Appendix 1) were examined, compared to the taxon character values of Table 2, and any departures noted. Ten herbarium specimens of New Zealand endemic *Lachnagrostis* (Appendix 1) were used to further assess the range of palea to lemma length ratio in this group.

Scanning Electron Microscope (SEM) images of the lemma epidermis from the largely unpublished work of the late Surrey Jacobs (1946–2009), formerly of the National Herbarium of New South Wales (NSW) were

examined and compared for a range of South African and Australasian *Agrostis* and *Lachnagrostis* collections at NSW. The SEM images were obtained during 1985–1986 in accordance with Jacobs (2001). A few SEM images of additional taxa were more recently made at The University of Melbourne.

Comparisons between genera for the selected characters were made to assess which were most

consistent in segregating taxa. New combinations were made in *Lachnagrostis* where character states suggested taxa were better placed.

## Results

A number of spikelet morphological features have been, or are currently, used to segregate taxa into

**Table 2.** Key morphological features (derived from a range of type descriptions, floras and online databases) of native and introduced South African *Agrostis*, *Lachnagrostis* and *Polypogon* taxa compared to a selection of Australasian taxa

Taxon <sup>1</sup>	Panicle form	Spikelet disarticulation <sup>2</sup>	Awned glumes	Glume surface <sup>3</sup>	Rachilla extension	Lemma length (mm)	Lemma hairiness	Palea to lemma length ratio <sup>4</sup>	Lemma awn length (mm)	Lemma awn attachment <sup>5</sup>	Anther length (mm)
South Africa											
<i>A. aristulifera</i> <sup>6</sup>	contracted	above	no	smooth	absent	1.5	glabrous	0.75, 0.90 <sup>7</sup>	0–1.0	> 90	?
<i>A. bergiono</i>	open	above	no	smooth	absent	1.5–2.5	glabrous	0.80	0–2.0	50	1.0
<i>A. continuata</i> <sup>8</sup>	contracted	above	no	scabl	present	2.1	sparse	0.33–0.50	4.2	< 25 <sup>9</sup>	1.6
<i>A. eriontho</i>	contr-open	above	no	smooth	absent	3.0–3.5	covered	0.90	4.0	40–50 <sup>9</sup>	2.0
<i>A. huttonioe</i> <sup>10</sup>	contracted	above	no	smooth	present	2.5	glabrous	0.95	0–0.5	> 66	1.0
<i>A. notolensis</i>	contracted	above	no	scabl	absent	2.1	glabrous	0.25–0.33	2.1	< 10 <sup>9</sup>	1.0
<i>A. polypogonoides</i>	contracted	above	yes	scabl	absent	2.1	moderate	0.90	3.0	50	1.5
<i>A. suavis</i> <sup>11</sup>	open	above	no	smooth	present	3.5	covered	0.90	5.0–6.0	40–50 <sup>9</sup>	?
<i>A. subulifolio</i> <sup>12</sup>	open	above	no	smooth	absent	1.7–2.7	glabrous	0.66	0–1.5	33	1.5
* <i>A. gigonteo</i>	open	above	no	smooth	absent	1.5–2.0	glabrous	0.50–0.65	rarely present		1.0–1.5
* <i>A. montevidensis</i>	open	above	no	smooth	absent	1.5–2.0	glabrous	0.08	2.0–2.5	66–75	0.8
<i>L. borbuligero</i>	open	above	no	smooth	present	2.7–5.0	moderate	0.75	3.0–6.0	10	2.6
<i>L. lochnontho</i>	contracted	above	no	smooth	absent	1.5–2.0	covered	0.80–0.95	0–0.5	90	0.5–0.8
<i>L. schlechteri</i>	open	above	no	smooth	present	2.0–2.5	moderate	0.66–0.90	4.0	50	1.9
<i>P. griquensis</i> <sup>13</sup>	contracted	below	yes	scabl	absent	1.0	glabrous	0.66–0.75	0.4–0.5	> 90	0.3
<i>P. strictus</i>	spiciform	below	yes	scabrous	absent	1.5	glabrous	1.00	5.0–10.0	> 90	0.3–0.7
* <i>P. monspeliensis</i>	spiciform	below	yes	scabrous	absent	0.9–1.5	glabrous	0.90	0–2.0	> 95	0.4–0.7
* <i>P. viridis</i> <sup>13</sup>	contracted	below	no	scabrous	absent	0.9–1.0	glabrous	1.00	absent		0.4–0.5
Australasia											
<i>A. oustroliensis</i> <sup>14</sup>	open	above	no	smooth	absent	1.7–2.0	glabrous	0	rarely present		0.2–0.5
<i>A. dyeri</i> <sup>15</sup>	open	above	no	smooth	absent	2.3–3.3	glabrous	0.07	rarely present		0.6–1.2
<i>A. imbecillo</i> <sup>15</sup>	contracted	above	no	smooth	absent	1.5–1.9	glabrous	0.06–0.10	absent		0.6–1.0
<i>A. muelleriono</i> <sup>14,15</sup>	contracted	above	no	smooth	absent	1.3–2.0	glabrous	0.17	rarely present		0.5–0.8
<i>A. muscoso</i> <sup>15</sup>	contracted	above	no	smooth	absent	1.2–1.4	glabrous	0.16–0.30	absent		0.4–0.6
<i>A. pollescens</i> <sup>15</sup>	open	above	no	smooth	absent	1.2–1.8	glabrous	0.30–0.33	absent		0.4–0.7
<i>A. porviflora</i> <sup>14</sup>	open	above	no	smooth	absent	1.5–2.0	glabrous	0–0.13	absent		0.3–0.5
<i>A. petriei</i> <sup>15</sup>	open	above	no	smooth	absent	2.0–2.6	glabrous	0.08	2.0–3.0	50	1.3–1.8
<i>A. propinquo</i> <sup>14</sup>	open	above	no	smooth	absent	1.3–2.0	glabrous	0–0.08	absent		< 0.5
<i>A. subuloto</i> <sup>15</sup>	contracted	above	no	cilio-scabr	absent	1.3–1.6	glabrous	0.25	rarely present		0.5–0.7
<i>A. venusto</i> <sup>14</sup>	open	above	no	smooth	absent	1.5–2.3	glabrous	0–0.08	2.2–5.0	10–50	0.2–0.6



**Table 2 cont.** Key morphological features (derived from a range of type descriptions, floras and online databases) of native and introduced South African *Agrostis*, *Lachnagrostis* and *Polypogon* taxa compared to a selection of Australasian taxa

Taxon <sup>1</sup>	Panicle form	Spikelet disarticulation <sup>2</sup>	Awned glumes	Glume surface <sup>3</sup>	Rachilla extension	Lemma length (mm)	Lemma hairiness	Palea to lemma length ratio <sup>4</sup>	Lemma awn length (mm)	Lemma awn attachment <sup>5</sup>	Anther length (mm)
<i>L. adamsonii</i> <sup>14</sup>	open	above	no	smooth	present	2.0-2.5	glabr-slight	0.90	1.5-3.5	66-90	0.4-0.7
<i>L. aemula</i> <sup>14</sup>	open	above	no	smooth	present	1.8-3.0	covered	0.90	5.0-10.0	25-60	0.6-1.2
<i>L. billardierei</i> <sup>7,15</sup>	open	above	no	smooth	present	2.5-4.5	glabrous	0.80	5.0-9.0	30-45	0.5-1.0
<i>L. deflexa</i> <sup>14</sup>	open	above	yes	fine scabl	present	2.2-2.7	glabr-slight	0.70-0.90	4.5-6.5	45-65	0.5-0.7
<i>L. filiformis</i> <sup>14,15</sup>	open	above	no	smooth	present	1.5-3.5	mod-sparse	0.80	3.5-5.5	45-55	0.2-0.5
<i>L. limitanea</i> <sup>14</sup>	open	above	no	micro scabl	present	1.0-2.0	glabrous	0.90-0.95	absent		0.6
<i>L. littoralis</i> <sup>15</sup>	open	above	no	smooth	present	1.8-2.5	moderate	0.95	3.0-6.0	50	0.4-0.7
<i>L. leptostachys</i> <sup>15</sup>	open	above	no	spars scabl	present	2.5-3.0	moderate	0.50-0.66	4.0-6.0	50-66	0.8-1.2
<i>L. lyallii</i> <sup>15</sup>	open	above	no	smooth	variable	2.0-2.5	covered	0.50-0.95	2.0-6.0	50	0.6-1.2
<i>L. meionectes</i> <sup>14</sup>	open	above	no	smooth	present	2.0-2.5	covered	0.90	2.0-4.0	70-80	1.0
<i>L. morrisii</i> <sup>14</sup>	open	above	no	smooth	present	1.7-2.6	glabrous	0.80-0.95	0.2-1.5	95	0.4-0.6
<i>L. pilosa</i> <sup>15</sup>	open	above	no	smooth	present	2.0-2.8	covered	0.50-0.60	4.5-8.5	50	0.6-1.2
<i>L. rudis</i> <sup>14</sup>	open	above	no	scabl	present	1.1-2.2	glabr-slight	0.95	0-1.4	70-95	0.5-0.7
<i>L. striata</i> <sup>15</sup>	contracted	above	no	smooth	present	1.2-2.0	covered	0.66-0.95	0.2-2.0	66	0.2-0.5
<i>P. tenellus</i> <sup>15</sup>	contracted	below	yes	scabl-cilio	absent	2.0-2.5	glabrous	0.50	13.5-19.0	50	0.3-0.4 <sup>16</sup>
<p>* naturalised introduction; 1 character information for type subspecies or variety only; 2 disarticulation point refers to above or below the glumes; 3 excluding the usually scabrous keel; assumed smooth if not described; scabl = scaberulous, scabr = scabrous, spars = sparsely, cilio = ciliate 4 a palea to lemma length ratio of 0.90 is used where the original description of palea is 'subequal' or 'a little shorter than lemma' 5 % lemma length from base 6 considered by Björkman (1960) to be a separate though closely related species to <i>A. bergiana</i> 7 values derived from the descriptions of Rendle (1899) and Björkman (1960) respectively 8 considered by most authors to be synonymous with <i>A. natalensis</i> 9 awn attachment is described as 'supra basin' (above base) for <i>A. continuata</i>, as 'recta supra basin' (just above the base) for <i>A. natalensis</i> and as 'v. infra medium' or 'paulo infra medium' (a little below the middle) for <i>A. eriantha</i> and <i>A. suavis</i> and is here assumed to be in the lower quarter, lower tenth and 40-50% of the lemma, respectively 10 considered by most authors to be synonymous with <i>L. lachnantha</i> 11 considered by some authors to be synonymous with <i>A. eriantha</i> 12 considered by some authors to be synonymous with <i>A. bergiana</i> 13 considered here to be <i>Polypogon</i> as for Gibbs Russell et al. (1990) 14 Australian taxa 15 New Zealand taxa 16 Current measurement (Darkin Swamp, 20.x.2011, A.J. Brown, 2553 (MEL)), taxon with one anther only</p>											

*Agrostis*, *Polypogon* and *Lachnagrostis*. These include the disarticulation point of the spikelet, the shape, surface and awned state of the glumes, the presence of a rachilla extension, the surface of the lemma and the length of the palea in relation to the lemma.

Glume shape and awns

Differentiation of *Polypogon* from *Agrostis* has been historically based on the presence of awns on the glumes. When Desfontaines (1798) originally described *Polypogon*, based on *P. monspeliensis*, he noted 'Calyx

exterior biglumis, uniflorus; glumis aristatis' (i.e. outer glumes two with a single floret; glumes awned) and 'Calyx interior brevior, biglumis; glumâ alterâ aristatâ; aristâ terminali' (i.e. the floret shorter than the outer glumes, with two glumes [lemma and palea]; alternate glume [lemma] with a terminal awn). Palisot de Beauvois (1812) described *Polypogon* as having glumes with a long awn ('longè setagera') arising just below emarginate, obtuse apices.

For South Africa, Stapf (1900) described the glumes of *P. monspeliensis* as 'shortly 2-lobed or emarginate ...

awn 2–3 lin. [4.2–6.4 mm] long' and those of *P. tenuis* as 'minutely or obscurely 2-lobed ... awn finely capillary, up to 1 lin. [2.1 mm] long'. Stapf (1897, 1900) noted an affinity of *A. griquensis* with *A. verticillata* ('sed gracilior' – but more slender), on the basis of their erect, narrow, sometimes interrupted 'spike-like, dense' panicles, which set them apart from the 'very lax, effuse or contracted' panicles of *Agrostis*. However, their lack of glume awns were the key criterion for Stapf (1900) to not transfer these taxa to *Polypogon*, even though he recognised that they also shared 'obtuse, mucronulate or emarginate' glumes, as opposed to the 'acute' glumes of the rest of the *Agrostis* in his key.

Awne glumes are seemingly not confined to *Polypogon*. Beetle (1945) described a number of North American *Agrostis* taxa (*A. ampla* Hitchc., *A. microphylla* Steud., *A. inflata* Beal and *A. kennedyana* Beetle) as having awne glumes. Likewise, in Australia, Vickery (1941) noted for *Deyeuxia forsteri* var. *aristata* Benth. (syn. *A. avenacea* J.F.Gmel., *L. filiformis* (G.Forst.) Trin.) that 'outer glumes produced into a long point' and Brown (2008) described *L. deflexa* A.J.Br. and *L. xcontracta* A.J.Br. as having 'each glume extended into a fine seta' (1.0–1.7 mm and 0.6–1.6 mm long, respectively). However, there is a distinct difference between the 'awn' of these taxa which are extensions of the keel from the acuminate point of the glume, and those of *Polypogon*, which arise from a terminal notch or just below the obtuse glume apex and usually appear to be a separate structure from the keel. Stapf (1900) noted that *A. polypogonoides* was the only South African *Agrostis* species recognised as having awne glumes: 'glumes subequal, lanceolate, acute, produced into fine fragile scabrid bristles (up to 1½ lin. (i.e. 3.2 mm) long)'. He stated that this taxon 'comes very near to *Polypogon*, the only difference being in the habit, and the absence of a terminal notch in the persistent glumes'.

### Spikelet disarticulation

Bentham (1887) appears to be the first author to unequivocally use the character of disarticulation of the spikelet below the glumes, so that part of the pedicel (or stipe) falls with it, as a diagnostic character for *Polypogon*. However, a much earlier reference by Ruchinger (1818) stating 'Cal. [calyx] di due valve, restato, con un solo fiore' (i.e. of two glumes, retained with a single flower) may

relate to the same feature and suggests that this trait had been observed by others. This disarticulation character was so unusual to Bentham (1887) that he erroneously placed *Polypogon* in Tribe Andropogoneae Dumort., with which only members of Tribe Paniceae R.Br. shared the feature in common. In recent grass treatments, the spikelet disarticulation point has become the major diagnostic feature that distinguishes *Polypogon* from *Agrostis* (Clayton & Renvoize 1986; Sell & Murrell 1996; Barkworth 2007).

For South Africa, Stapf (1900) described *Polypogon* spikelets as 'disarticulating from the pedicels' but was obviously unaware that both *A. griquensis* and *A. verticillata* possess this character (Table 1). Gibbs Russell et al. (1990) placed both taxa into *Polypogon*, stating that their transfer of *A. griquensis* to *P. griquensis* was on the basis that 'the entire floret plus a short stipe together form the disseminule'. Fish (2006) formally, though belatedly, transferred *A. griquensis* to *P. griquensis*. In Clayton et al. (2006 onwards)'s treatment of *A. polypogonoides* as *P. polypogonoides* (Stapf) Forsan they describe it as having spikelets 'falling entire: deciduous with the pedicel' but as noted above, Stapf (1900) stated that *A. polypogonoides* has 'persistent glumes'.

### Glume surface

The surface of the glumes of *Polypogon* have been variously described (sometimes depending on the species) as minutely pilose (Trinius 1841), scaberulous (Stapf 1900), rough (Tutin 1962), rough with minute points (Hubbard 1968), scabrid (Tutin 1980), hairless but hispid or hairy and usually scabrous (Watson & Dallwitz 1992 onwards), scabrous, ciliate or with inflated bristles (Walsh & Entwistle 1994), asperulous (Clayton et al. 2006 onwards), echinate, scabridulous or hispidulous (Barkworth 2007) and hispid or puberulous (Keshavarzi et al. 2007), and often with ciliate margins. Although descriptions vary between species and sometimes within the same species, these observations reflect a general roughness or coarse hairiness to the glume surfaces.

The glumes of the majority of *Agrostis* are described as smooth or shiny and glabrous (Edgar & Forde 1991; Harvey 2007; Watson & Dallwitz 1992 onwards; Clayton et al. 2006 onwards), but this difference in character does not appear to have ever been used to differentiate



between the two genera. This is likely due to the occasional scaberulous glume surfaces in *Agrostis*. For instance, according to Barkworth et al. (2007), the glumes of a few North American *Agrostis* are scabrous, though only towards the apices (e.g. *A. hyemalis* (Walter) Britton, Sterns & Poggenb., *A. exarata* Trin.) or are scabridulous across the body (e.g. *A. hendersonii* Hitchc., *A. microphylla* Steud.) or are very occasionally densely scabrous (e.g. *A. densiflora* Vasey).

The Australasian taxa of *Agrostis* and *Lachnagrostis* are likewise variable. Again, while most species have smooth glumes (except for the keels), a number are scabrous to some degree and many are occasionally sparsely scaberulous. Edgar and Forde (1991) describe the glumes of the subantarctic *A. magellanica* Lam. (syn. *P. mogellonicus* (Lam.) Finot) as finely scabrous and those of the New Zealand endemic, *A. subuloto* Hook.f. as ciliate-scabrous. In Australia, Vickery (1941) described the lateral faces of the glumes of *A. limitonea* J.M.Black (syn. *L. limitaneo* (J.M.Black) S.W.L.Jacobs) as microscaberulous, *A. rudis* Roem. & Schult. (syn. *L. rudis* (Roem. & Schult.) Trin.) as scabrous and *A. plebeia* R.Br. (syn. *L. plebeia* (R.Br.) Trin.) as slightly scaberulous. Brown and Walsh (2000) described *A. collicola* D.J.Morris (syn. *L. collicola* (D.J.Morris) S.W.L.Jacobs) as having densely and finely scaberulous glumes and Brown (2008) described *L. deflexo* and *L. xcontracto* as having glumes with finely scaberulous lateral surfaces and marginal cilia. Although, the glume surfaces of these Australian taxa may approach the hispid and ciliate glumes of *Polypogon*, most other features of the spikelet, including glume shape are clearly not *Polypogon*-like. By contrast, the Australian *P. tenellus* R.Br. has both the glume characters of *Polypogon* (i.e. awned, scaberulous to ciliate glumes) and disarticulation of the spikelet below the glumes.

For South African taxa, Stapf (1900) included *A. natolensis* and *A. polypogonoides* in his descriptions of scaberulous glumes as he did for *P. monspeliensis*, *P. tenuis*, *A. griquensis* (syn. *P. griquensis*) and *A. verticillata* (syn. *P. viridis*). Current cursory examination of specimens of these species (Appendix 1) and other *Agrostis*/*Lachnagrostis* taxa shows a wide range in surface covering but suggests that utilisation of a uniform and detailed set of criteria and descriptions across replicated taxon examples may reveal some generic diagnostics. For example, the densely ciliate margins of many

*Polypogon* species are rarely, if ever, observed in *Agrostis* or *Lachnagrostis*.

### Palea to lemma length ratio and rachilla extension

Jacobs (2001) characterised *Lachnagrostis* as differentiated from *Agrostis* by 'i) a palea almost as long as the lemma (always > 50%); ii) an obvious and well-developed hairy rachilla extension that, with the apical hairs, may be almost as long as the lemma; and iii) a tendency for the whole inflorescence to become detached and act as the diaspore, though this character is not always obvious and appears to be suppressed in some species'. As the latter feature is not readily determined from herbarium specimens and none of the descriptions of South African taxa mention such, it cannot be used to discriminate between genera in the current analysis.

Comparison of Australasian *Agrostis* and *Lachnagrostis* taxa (Table 2) show clear differences between genera in palea to lemma length ratio and rachilla extension production (except sometimes in *L. lyallii* (Hook.f.) Zotov) (i.e. small paleas and no rachilla extension in *Agrostis* and long paleas and a rachilla extension in *Lachnagrostis*). Such is not the case for the South African taxa (native and exotic). Among *Agrostis*, only *A. natolensis* and *A. montevidensis* conform to the normal character states. Although lacking a rachilla extension, *A. bergiana* (including *A. aristulifera*), *A. eriantha* and *A. polypogonoides* have long paleas and *A. subulifolia* and *A. gigantea* have moderately long paleas. In this respect they have similar characters to *Polypogon* (Table 2). On the other hand, *A. continuata* has the small paleas of *Agrostis* but does produce a rachilla extension. The two taxa, *A. huttonioe* and *A. suavis*, generally regarded as synonymous with *L. lochnantha* and *A. eriantha* respectively, have the two character states of *Lachnagrostis*. However, among the three South African *Lachnagrostis* taxa, only *L. barbuligera* and *L. schlechteri* conform to normal character states, for even though *A. lochnantha* was transferred to *Lachnagrostis* by Rúgolo de Agrasar and Molina (2002), it usually does not have a rachilla extension. Of ten *L. lochnantha* specimens examined in the current study (Appendix 1), only one showed any rachilla extension and even this observation was inconsistent among spikelets.



**Table 3.** Details of samples and their Scanning Electron Microscope images (Figs. 1, 2 and 3) for a selection of native and introduced South and East African and native Australasian *Agrostis*, *Polypogon* and *Lachnagrostis* taxa and the lemma epidermis pattern present (using the classification of Jacobs 2001)

Former taxon name <sup>1</sup>	Updated taxon name <sup>2</sup>	Lemma base image <sup>3</sup>	Lemma epidermis pattern	Location	Collector	Collection date	Herb. no. <sup>10</sup>
<i>A. bergiono</i> var. <i>mutica</i> <sup>4</sup>	<i>A. bergiono</i>	Fig. 1a	trichodium net	Capcolonie, S. Afr.	R. Schlechter 2344	15.iii.1893	NSW852639
<i>A. neesii</i> ( <i>L. lochnonθο</i> ) <sup>5</sup>	<i>A. bergiono</i>	not shown	trichodium net	Austro-Africanæ	R. Schlechter 10081	22.i.1897	NSW883631
<i>A. notolensis</i>	<i>A. continuato</i> <sup>6</sup>	Fig. 1b	trichodium net	Olifant River, S. Afr.	R. Schlechter 4042	23.xii.1893	NSW852648
<i>A. montevidensis</i>	–	Fig. 1c	trichodium net	Punta Gorda, Uruguay	C. Osten 5310	20.ii.1910	NSW852646
<i>A. giganteo</i>	–	Fig. 1d	raised margins	Yarnton, UK	C.E. Hubbard 10671	20.vii.1941	NSW883624
<i>A. venusto</i>	–	Fig. 1e	trichodium net	Hedley Tarn, NSW	J. Thompson 2859	6.ii.1978	NSW548381
<i>A. porvifloro</i>	–	Fig. 1f	trichodium net	Queenstown – Strahan, Tas.	J. Vickery s.n.	20.i.1949	NSW7495
<i>A. oustrolensis</i>	–	Fig. 1g	trichodium net	Mt Wellington, Tas.	L. Rodway s.n.	i.1893	NSW548376
<i>A. propinquo</i>	–	Fig. 1h	trichodium net	One Tree Hill, Vic.	J. Vickery s.n.	22.i.1935	NSW546266
<i>A. muelleriono</i>	–	SJ Fig. 1a	trichodium net	Mt Somers, NZ	V.D. Zotov s.n.	3.iii.1938	NSW548447
<i>A. lochnonθο</i>	<i>L. lochnonθο</i>	Fig. 2a	raised margins	Witzieshoek, S. Afr.	P.C.V. du Toit s.n.	21.iii.1975	NSW852644
<i>A. schlechteri</i> <sup>4</sup>	<i>L. schlechteri</i>	Fig. 2b	smooth	Villiersdorp, S. Afr.	R. Schlechter 9909	8.i.1896	NSW852652
<i>A. suavis</i> <sup>4</sup> [isotype]	<i>L. erionθο</i> <sup>3</sup>	Fig. 2c	raised margins	Van Reenen, S. Afr.	J. Medley Wood 8913	29.i.1903	NSW852653
<i>A. erionθο</i>	<i>L. erionθο</i> <sup>3</sup>	not shown	raised margins	Tafelkop, S. Afr.	N.J. Devenish 3843	1982	PRE664945
<i>A. polypogonoides</i> <sup>4</sup>	<i>L. polypogonoides</i> <sup>3</sup>	Fig. 2d	smooth	Villiersdorp, S. Afr.	R. Schlechter 9915	8.i.1896	NSW852650
<i>A. odomsonii</i>	<i>L. odomsonii</i>	Fig. 2e	smooth	Melbourne, Vic.	Adamson 226	12.xi.1853	NSW546289
<i>A. ovenoeco</i>	<i>L. filiformis</i>	Fig. 2f	smooth	Grafton, NSW	M.J.E. Squire s.n.	1.xi.1932	NSW134519
<i>A. meionectes</i>	<i>L. meionectes</i>	Fig. 2g	raised margins	Upper Betts Ck, NSW	J. Thompson 2822	5.ii.1978	NSW548653
<i>A. oemulo</i>	<i>L. oemulo</i>	Fig. 2h	smooth	Llanthgothlin, NSW	E.N. McKie 2510	7.i.1948	NSW13387
<i>A. billfordieri</i>	<i>L. billfordieri</i> <sup>7</sup>	SJ Fig. 1c	smooth	Dolphin Sands, Tas.	A.M. Buchanan 4763	10.xii.1984	NSW532486
<i>A. borbuligero</i>	<i>L. borbuligero</i> <sup>8</sup>	Fig. 3a	trichodium net	Bethlehem, S. Afr.	Ellis 2404	21.iii.1975	NSW852637
<i>A. borbuligero</i>	<i>L. borbuligero</i> <sup>8</sup>	not shown	trichodium net	Tschlangana Valley, S. Afr.	Jacot-Guillamod 3737	8.i.1960	PRE40497
<i>A. b. var. longipiloso</i>	–	Fig. 3b	trichodium net	Bethlehem, S. Afr.	Roberts 3280	24.i.1965	PRE38919
<i>A. burtii</i>	<i>A. kilimondschorico</i>	Fig. 3c	trichodium net	Belgian Congo	J. Louis 5399	20.viii.1937	NSW883629
<i>A. trochophyllo</i>	–	Fig. 3d	trichodium net	Mt Kenya, Kenya	Schelte 2879	29.viii.1949	NSW883632
<i>A. mildbreodii</i>	<i>A. quinqueseto</i>	not shown	trichodium net	Congo Belgica	J. Louis 5371	viii.1937	NSW883628
<i>P. monspeliensis</i>	–	Fig. 3e	smooth	Fish Creek, Vic.	A. Paget 1148	5.xii.1994	MEL2026751
<i>A. schimperiono</i>	<i>P. schimperiono</i>	Fig. 3f	raised margins	Lushoto District, Tanzania	H. Faulkner 4475	19.xi.1970	NSW883630
<i>A. griquensis</i> <sup>4</sup>	<i>P. griquensis</i>	Fig. 3g	smooth	Bloemfontein, S. Afr.	G. Potts 2467	6.x.1917	NSW852640
<i>A. semiverticillato</i>	<i>P. viridis</i>	Fig. 3h	raised margins	Tarrabandra, NSW	E. McBarron 5278	8.xi.1950	NSW13651

1 name under which SEM imaged

2 current name

3 comb. nov. made in this paper

4 name provided by Goossens and Papendorf (1945) for duplicates of these collections

5 a specimen sheet identified as *Agrostis neesii* (*A. lochnonθο*) at the Zürich Herbaria bears similar details to this sample and is probably a duplicate (Western Cape Province, Konde Bokkevelt in monte Tafelberg, 5000 ft., 22.i.1897, R. Schlechter 10081, Z-000073075)

6 name given in synonymy but some character distinctions may warrant review of this taxon

7 subsp. *tenuiseta*

8 synonymous name but taxon rejected in this paper as a species of *Lochnagrostis*

9 lemma base images relate to those in the current paper except for SJ = Jacobs (2001)

10 NSW specimens imaged by S.W.L. Jacobs; PRE and MEL specimens imaged by T. Schuster and H. Merrylees

The palea to lemma length ratio for Australasian *Agrostis* range from 0–0.33 (Table 2). According to the measurements of Björkman (1960), palea to lemma length ratio among Eurasian *Agrostis* (after discarding taxa transferred to *Neoschischkinia*) varied from 0–0.70. Among taxa with the highest values were *A. stolonifera* L. and *A. gigantea*. Reported values by Jacobs and Brown (2009) of all the Australian *Lochnogrostis* show palea to lemma length ratio of at least 0.75, except for the rare and possibly extinct *L. drummondiana* (Steud.) S.W.L. Jacobs, at 0.65. However, the descriptions of New Zealand *Lochnagrostis* by Edgar (1995) show a wide range of palea to lemma length ratio from 0.50–0.95. Current measurements of 2–4 specimens (Appx. 1) of taxa with the shortest paleas, gave ranges in palea to lemma length ratio of 0.50–0.70 for *L. piloso* (Buchanan) Edgar, 0.63–0.66 for *L. leptostochys* (Hook.f.) Zotov, 0.60–0.78 for *L. lyallii* and 0.81–0.88 for *L. striato* (Colenso) Zotov. Current measurement of the lemma and palea of specimens of *Agrostis bergiano* and *A. continuata* (Appx. 1) resulted in palea to lemma length ratio of 0.76 and 0.35, respectively, and confirmed reported values (Table 2).

It therefore appears that neither the presence of a rachilla extension or palea to lemma length ratio can be exclusively used to segregate all the South African taxa into current circumscriptions of *Agrostis* and *Lochnagrostis*.

### Other gross morphological characters

Panicle form, lemma length and hairiness, awn length and attachment point, and anther length are often variable within and between genera, although some characters show a trend towards a common state within a genus (Table 2).

The panicle form for *Polypogon* is always contracted and spike-like (spiciform), though sometimes interrupted, while *Lochnogrostis* displays loosely contracted to open panicles. Panicles of *Agrostis* vary widely between taxa, from spiciform to open.

Lemma length varies so widely within genera (Table 2), that it does not serve well as a discriminating character between them.

The lemmas of all Australasian *Agrostis* taxa are glabrous and smooth, whereas the lemmas of the majority of *Lochnogrostis* are hairy to some extent

or finely scaberulous in part (although there are exceptions) (Table 2). This general rule also applies to *Agrostis* (and to *Polypogon*) in the northern hemisphere, with a few exceptions in *A. conina* L. and *A. vinealis* Schreb. with their minutely pubescent bases and in *A. costellona* Boiss. & Reut. with its occasional hairs in the lower half (Harvey 2007). Many species are also observed to sometimes display scabridulous or scabrous lemmas (e.g. *A. elliottiana* Schult., *A. howellii* Scribn. and *A. rossioe* Vasey). A further group of Himalayan to Chinese *Agrostis* (including *A. pilosula* Trin., *A. pendryi* Paszko, *A. griffithiana* (Hook.f.) Bor and *A. munroana* Aitch. & Hemsl.) are unusual in having lemmas covered in pilose hairs (Shenglian & Phillips 2006; Paszko 2014). Among the South African *Agrostis*, *A. eriantha*, *A. suavis* and *A. polypogonoides* have moderately to very hairy lemmas, as do *L. borbuligera*, *L. schlechteri* and *L. lachnantha*. The original description of *A. huttoniae* (as *Colamagrostis huttoniae* (Hack.) by Hackel (1905) indicated that the lemma is glabrous, whereas later descriptions of a hairy lemma (e.g. Launert 1971) may be referable to *L. lachnantha* when treated in synonymy. Stapf (1897) described *A. continuata* as being pilose along the secondary nerves of the lemma, while the lemmas of *A. natalensis* are presumably glabrous.

Almost all Australasian *Lochnagrostis* have lemma awns (albeit that some are greatly reduced) whereas only a quarter of Australasian *Agrostis* taxa (*A. boormanii* Vickery, *A. magellonico* Lam., *A. oresbio* Edgar, *A. petriei* Hack. and *A. venusto* Trin.) regularly have lemmas with a basal to mid-dorsal awn. A number of other species occasionally have very fine to early deciduous lemma awns. For North America, Harvey (2007) notes about a third of the endemic species to have regularly awned lemmas and a further third to be sometimes awned. Substantial lemma awns are found in the South African *A. continuata* and *A. natalensis* (arising from the lower dorsal region) and *A. eriantha* and *A. suavis* (arising from the mid-dorsal region) and in the South American *A. montevidensis* (arising from the upper-dorsal region). The remaining *Agrostis* taxa are awnless or have insubstantial awns. Within *Lochnogrostis* only *L. lachnantha* (like *A. huttoniae*) has an occasional minute sub-terminal lemma awn. All *Polypogon* taxa have sub-terminally awned lemmas, except for *P. viridis*, but the awns range from being long, robust and twisted in *P. tenellus* R.Br. to minute in *P. griquensis*.



Anther length in *Agrostis* and *Lachnagrostis* varies considerably (Table 2), although all the South African taxa (where known), other than *L. lachnantha*, have anthers of at least 1 mm. The anthers of *Polypogon* tend to be 0.5 mm or less. Descriptions of anther length in *P. strictus* are lacking but current measurements (Appendix 1) ranged from 0.3–0.7 mm.

### Lemma epidermis features

Björkman (1960) described a common lemma epidermis feature of *Agrostis* as a 'trichodium net': 'where the beams of two laterally adjacent cells alternate, resulting in a fine-meshed network over the surface of the lemma'. He developed a 4-fold categorisation: 1) network fully developed, 2) network only fragmentarily developed, 3) without a developed network but with a tendency toward it and 4) entirely without a network or tendency toward it. Widén (1971) utilised the trichodium net in his work with *Agrostis* in eastern Fennoscandia but introduced additional categories, related to the relative thickness of the cell walls, to make a 7-fold system. Jacobs (2001), when describing the lemmatal epidermal structure of the Australian *Agrostis*, *Lachnagrostis* and *Deyeuxia* in comparison to *Calamagrostis*, also used the trichodium net pattern but only described three types: i) the trichodium net pattern, ii) 'raised margins of epidermal cells, with or without prickles', and iii) 'a comparatively smooth epidermis, the cell walls appearing more or less wavy in outline but the margins flush with the surface, prickles present or absent and macrohairs present or absent'. The 'raised margins' pattern (ii) of Jacobs (2001) is probably comparable to the 'without a developed network' but 'a tendency toward' (iii) of Björkman.

SEM images of basal lemma surfaces show distinctive trichodium net patterns for *A. bergiana*, *A. continuata*, *A. montevidensis* and all the tested Australasian *Agrostis* taxa (Fig. 1a–c, e–h). This is in keeping with most *Agrostis* species in other parts of the world, as reported by Björkman (1960), Widén (1971) and Finot et al. (2011) among others (e.g. *A. canina* L., *A. tenuis* Sibth. (syn. *A. capillaris* L.) and *A. rupestris* of Europe; *A. hyemalis* (Walt.) B.S.P. and *A. idahoensis* Nash of North America; *A. inaequiglumis* Griseb. and *A. rigidula* Steud. (syn. *A. infirma* Buse.) of Asia, *A. brachyathera* Steud. and *A. ramboi* Parodi of South America and *A. dyeri* Petrie and *A. petriei* Hack. of New Zealand). As *A. canina* is the type

of *Agrostis*, the presence of a trichodium net should be taken as the typical state for the genus. Notable exceptions are the widely introduced *A. stolonifera*, *A. castellana* and *A. gigantea* (Fig. 1d), which have either fragmentary (as in the first two species) or only a tendency (as in the last species) for trichodium networks. Interestingly, taxa with under-developed trichodium networks tend to have higher palea to lemma length ratio and may represent species divergence from *Agrostis* to *Polypogon*, *Lachnagrostis* or other Agrostidinae genera. On the other hand, a group of African taxa, including *A. bergiana*, show trichodium networks on the palea as well as on the lemma (Björkman 1960) but also have a relatively long palea. Superficially, *A. bergiana* is similar to *A. stolonifera* which also has an erect or ascending habit, a contracted panicle, relatively long paleas and anthers and a diminutive awn (if present) and is suggestive of a close relationship. However, the distinctive differences in lemma epidermis structure between the two taxa would indicate otherwise.

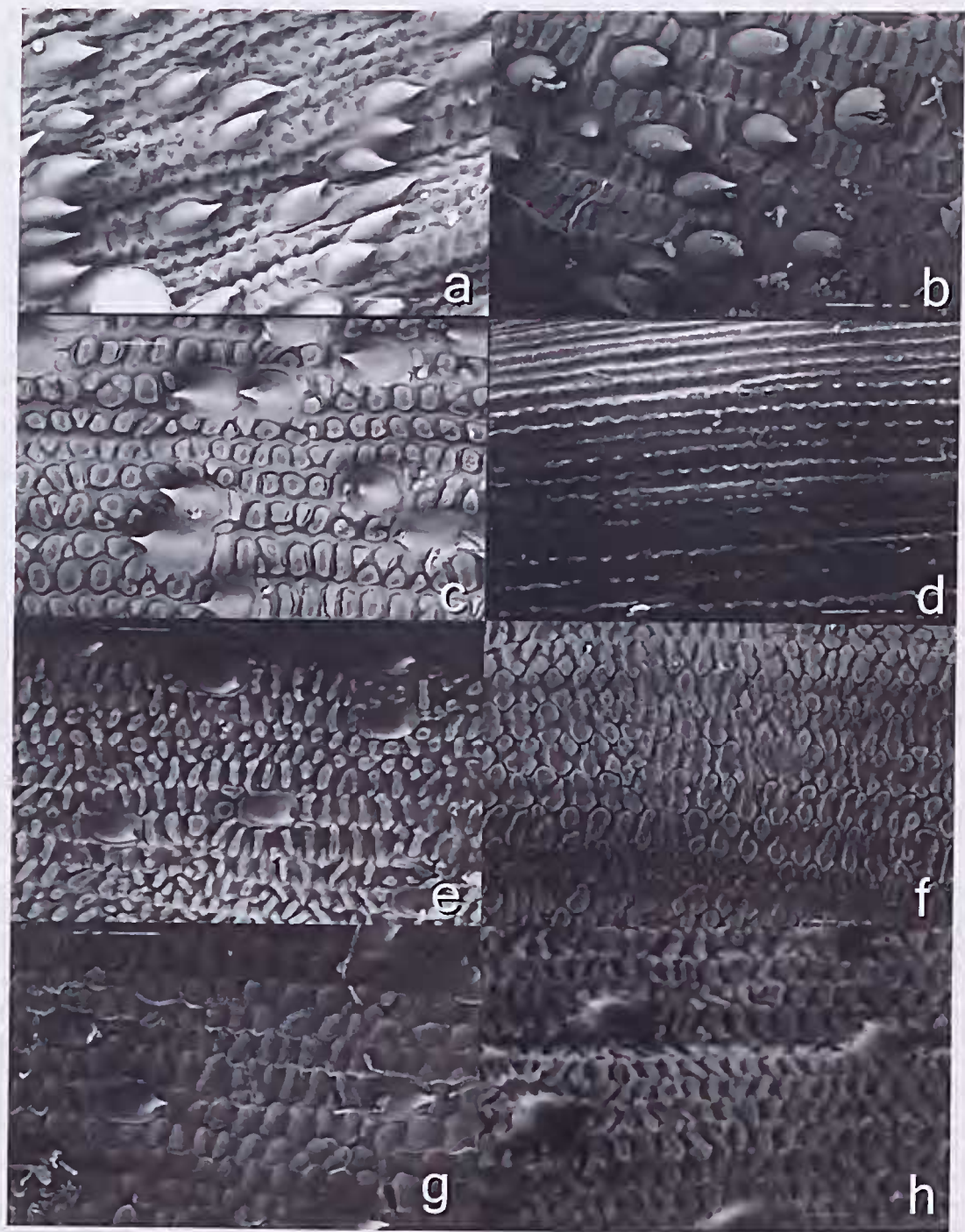
All of the tested Australasian (Fig. 2e–h) and South African *Lachnagrostis* (Fig. 2a–b), except for *L. barbuligera* (Fig. 3a–b), show an absence of a trichodium net, even though there are some differences in the epidermis between species. In addition, the South African *A. polypogonoides* and *A. eriantha* also lack a trichodium net (Fig. 2c–d).

Björkman (1960) found that *Polypogon* species (including *P. monspeliensis* and *P. semiverticillatus*), lacked a trichodium network on their lemma epidermis, while species of *Chaetotropis* did possess a trichodium net. The lack of such a network in the recent SEM images of *A. semiverticillata* and *A. griquensis* (Fig. 3g–h) confirms their non-*Agrostis* status and supports their placement in *Polypogon* as *P. viridis* and *P. griquensis*, respectively. Jacobs (2009) considered *P. viridis* to belong in *Agrostis*, which may be explained by his erroneous comment that *A. viridis* 'has a classic *Agrostis* spikelet, including the trichodium net ... and the characteristic lemma surface of *Agrostis* s. str.'.

## Discussion

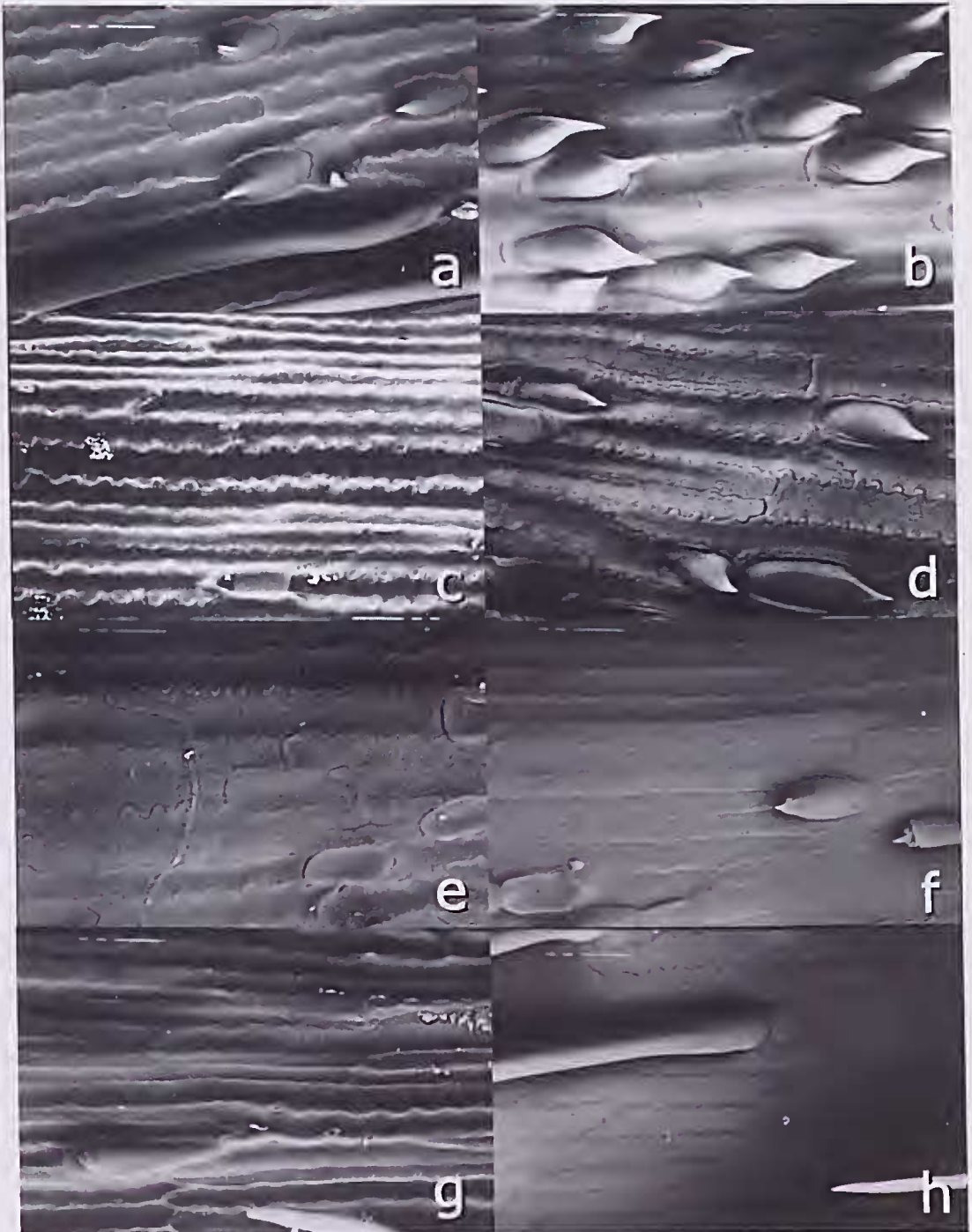
### *Agrostis natalensis* and *A. continuata*

Clayton (1970) considered *Agrostis natalensis* to be synonymous with *A. continuata* Stapf of Malawi along with *A. radula* Mez of Malawi and *A. makoniensis* Stent



**Figure 1.** Scanning Electron Microscope images (x1800) of the lower lemma epidermis of *Agrostis* from South Africa and Australasia: **a.** *A. bergiana* (SJi); **b.** *A. natalensis* (SJi); **c.** *A. mantevidensis* (SJi); **d.** *A. gigantea* (SJi); **e.** *A. venusta* (SJi); **f.** *A. parviflora* (SJi); **g.** *A. australiensis* (SJi); **h.** *A. prapinqua* (SJi). See Table 3 for voucher information; SJ = Jacobs pattern classification.





**Figure 2.** Scanning Electron Microscope images ( $\times 1800$ ) of the lower lemma epidermis of *Lachnagrostis* taxa from South Africa and Australasia: **a.** *Agrostis lochnonθο* (syn. *Lochnagrostis lochnonθο*) (SJii); **b.** *A. schlechteri* (syn. *L. schlechteri*) (SJiii); **c.** *Agrostis suavis* (syn. *L. erianthο*) (SJii); **d.** *A. polypogonoides* (syn. *L. polypogonoides*) (SJiii); **e.** *A. odomsonii* (syn. *L. odomsonii*) (SJiii); **f.** *A. avenaceo* (syn. *L. filiformis*) (SJiii); **g.** *A. meionectes* (syn. *L. meionectes*) (SJii); **h.** *A. oemula* (syn. *L. oemulo*) (SJiii). See Table 3 for voucher information; SJ = Jacobs pattern classification.

& Rattray of southern Rhodesia (Zimbabwe), and Launert (1971) included *A. whytei* C.E.Hubb. of Malawi in synonymy. However, Hubbard (1937) considered that *A. natalensis* could be distinguished from *A. continuata* by its 5- or 6-noded culms (compared to 2- or 3-noded), its larger spikelets (5.3–6.4 mm in length compared to 4.2–5.3 mm) and its linear-oblong glumes (compared to oblong). Stapf (1897) described the lemmas of *A. continuata* as being thinly pubescent along the nerves, but did not do so for *A. natalensis*. Other differences between the taxa are the longer paleas, awns and anthers and generally higher awn attachment of *A. continuata* (Table 2). The production of a rachilla extension from 0.5–4 mm long, appears common for *A. continuata* but is missing for *A. natalensis*.

Unusually for *Agrostis* (and *Lachnagrostis*), both taxa have erect, spike-like, lobed panicles with branches in dense, oblong fascicles, lemma nerves that extend beyond the apex into fine mucros and a robust, scabrid, straight to subgeniculate, lemmatal awn that tapers at both ends (see Plate 195 in Wood 1904). Apart from these features, the presence of a trichodium net on the lemma epidermis indicates that they do not belong in *Lachnagrostis*. Stapf (1897) comments that *A. natalensis* is allied to the Malagasy *A. elliotii* Hack., the subantarctic *A. antarctica* Hook. f. (syn. *A. magellanica* Lam.) and a few South American species described by Nees von Esenbeck (1841a) under *Bromidium*. Future detailed study of this group of grasses may dictate one or more separate genera to *Agrostis*.

### ***Lachnagrostis lachnantha* (syn. *Agrostis lachnantha*), *A. huttoniae*, *A. neesii* and *A. papposa***

Although rachilla extensions are generally absent in *Lachnagrostis lachnantha*, the taxon conforms to *Lachnagrostis* in spikelet size, lemma hairiness, and palea to lemma length ratio. The closely related *Agrostis huttoniae* does have a rachilla extension, although Launert (1971) considered that this feature and the longer callus hairs described by Goossens and Papendorf (1945) could not be used to separate the two taxa, as he found many intermediate stages between them. However, as it is sufficiently different from *L. lachnantha* in its larger glumes (3 mm compared to 1.6–2.6 mm), lemmas (2.5 mm compared to 1.5–2 mm) and

anthers (1 mm compared to 0.5–0.8 mm), in addition to the presence of a rachilla extension, it should be considered as both a separate species and as a species of *Lachnagrostis*.

Trinius (1841) made the new combination *A. neesii* Trin. for the South African *Podosemum angustum* Nees but treated it as synonymous with *A. lachnantha* (syn. *P. lachnanthum* Nees). Nees von Esenbeck (1841b) described these taxa as similar but different in a number of features. These included, for *P. angustum*: 'i.e. flosculo glabro mutico' (glabrous, awnless lemmas) and 'i.e. processu calli distincto lineari barbato' (distinct and shortly bearded, rachilla extension) and for *P. lachnanthum*: a lemma with 'i.e. apice bidenticulata infra apicem brevissime setuligera calloque villosis' (short bristle arising from between two short teeth at the apex, surface villous hairy) and 'i.e. calli processu nullo aut obsoleto' (rachilla extension absent or minute). In these characters, *P. angustum* (syn. *A. neesii*) appears very similar to *A. huttoniae* and may represent the same entity. However, the herbarium specimen (MEL2386775) examined as *A. neesii* (Appendix 1) had a hairy lemma and lacked a rachilla extension and therefore appeared to conform to *L. lachnagrostis*. Note that the herbarium specimen (NSW883631) identified as *A. neesii* from which the lemma epidermis SEM image derived (not shown), and with a trichodium net, is actually a collection of *A. bergiana*, according to duplicate sheets at PRE and GRA examined by Goossens and Papendorf (1945).

Although Goossens and Papendorf (1945) placed the South African *A. papposa* Mez in synonymy with *A. huttoniae*, its position is not as clear. Mez (1922) describes it as having 'i.e. axis processus certe deest' (rachilla extension certainly missing), spikelets of 2.2 mm length and glabrous lemmas  $\frac{3}{4}$  the length of the glumes (i.e. 1.7 mm). Apart from the glabrous lemmas and the 'i.e. callus ... pilis longis papposa' (callus a long haired pappus, compared to the Stapf (1900) description of 'callus scantily bearded' for *A. lachnantha*), this taxon more nearly approaches *L. lachnantha* than *A. huttoniae*, but remains taxonomically uncertain until a more thorough examination can be made.

The lemma of *L. lachnantha* is distinct from the other South African *Agrostis*/*Lachnagrostis* taxa in only being 3-nerved. Almost all other *Agrostis* and *Lachnagrostis*, worldwide, have 5-nerved lemmas, except sometimes in a few species, including *A. capillaris*, *A. castellana*, *A.*



*gigantea*, *A. elliotiana* and *A. nipponensis* and in some Malagasy taxa (Edgar & Forde 1991; Clayton et al. 2006 onwards; Harvey 2007, Jacobs & Brown 2009). In some cases, the five nerves are somewhat indistinct and may lead to a description of only three or four.

### ***Lachnagrostis schlechteri*, *Agrostis suavis*, *A. eriantha* and *A. polypogonoides***

The presence of a rachilla extension, the high palea to lemma length ratio and the lack of a trichodium network on the lemma epidermis of *Lachnagrostis schlechteri* confirms its current generic placement. The last two characteristics, at least, indicate that *Agrostis suavis* and *A. polypogonoides* also belong to *Lachnagrostis*.

Goossens and Papendorf (1945) noted *A. polypogonoides* as having 'rachilla produced', even though Stapf (1900) noted 'rachilla not produced beyond the floret', in his original description. Hackel (1904) described *A. eriantha* as having 'rachilla non producta'. Current examination of herbarium specimens of both taxa (Appendix 1), found no evidence of a rachilla extension. Despite the lack of a rachilla extension, *A. eriantha* and *A. polypogonoides* display all the other main characters of *Lachnagrostis*, including diffuse panicles, large spikelets, hairy lemmas and geniculate awns.

After 'carefully' examining the types of *A. eriantha* and *A. suavis*, both morphologically and anatomically, Goossens and Papendorf (1945) concluded that they belong to the same species. However, they did not mention the difference in the presence or absence of a rachilla extension. On the other hand, as the illustration of the type for *A. suavis* in Wood (1908) does not feature a rachilla extension and the text indicates 'rachilla reduced to a fascicle of hairs scarcely ½ line [ca. 1 mm] long', such could easily have been overlooked.

In their observation of leaf anatomy across all the types and co-types of South African *Agrostis*, Goossens and Papendorf (1945) mention that *A. eriantha* was an exception in having a leaf that is 'fairly rigid and typically folded so that it appears ellipsoid or V-shaped when seen in cross section', but whether or not *A. suavis* was also found to be an exception is not stated. In the original descriptions by Hackel (1904) and Stapf (1908), respectively, the leaves of *A. eriantha* are 'i.e. plerumque complicatae' (mostly folded), while those of *A. suavis* are

'i.e. ex siccando plicate' (folded on drying out). However, without more distinct differences, it is probable that the two taxa are indeed the same species.

A SEM image of the lemma epidermis of *A. eriantha* (N.J. Devenish 3843 (PRE664945) – not shown) was found to be almost identical to that of *A. suavis* (Fig. 2c).

### ***Lachnagrostis barbuligera***

Although *Lachnagrostis barbuligera* has the gross morphological characters of the other South African *Lachnagrostis*, it has a trichodium net on its lemma epidermis (Fig. 3a and Jacot-Guillamod 3737 (PRE40497) – not shown). Björkman (1960) noted that a group of montane tropical African grasses, including *Agrostis alpicola* Hochst. and *A. sclerophylla* C.E.Hubb. from Abyssinia (Ethiopia), *A. burtii* C.E.Hubb. from the Belgian Congo, *A. dissitiflora* C.E.Hubb., *A. friesiorum* C.E.Hubb., *A. keniensis* Pilg., *A. mildbraedii* Pilg., *A. pilgeriana* C.E.Hubb., *A. trachyphylla* Pilg. and *A. volkensii* Stapf from Kenya and *A. kilimandscharica* Mez and *A. producta* Pilg. from Tanganyika (Tanzania), had long paleas (at least two-thirds the length of the lemma) and a trichodium net pattern (although fragmentary in the case of *A. pilgeriana*) on both their lemma and palea epidermes. Clayton (1970) treated *A. burtii* and *A. friesiorum* as synonymous with *A. kilimandscharica*; *A. alpicola* and *A. mildbraedii* as synonymous with *A. quinqueseta* (Steud.) Hochst.; and *A. dissitiflora* as synonymous with *A. gracilifolia* C.E.Hubb. Within this group, Phillips (1986) also identified *A. mannii* (Hook.f.) Stapf from highlands of the Cameroon and Fernando Po and *A. diffusa* S.M.Phillips from Ethiopia. The current study confirms a trichodium net pattern on the lemmas of *A. kilimandscharica* (Fig. 3c as *A. burtii*), *A. trachyphylla* (Fig. 3d) and *A. quinqueseta* (as *A. mildbraedii* – not shown).

Like *A. barbuligera*, the spikelets of most of these grasses also have a rachilla extension, tend to have pilose lemmas and basal or near-basal lemma awns. They therefore form a group of species that are distinct from both *Agrostis* and *Lachnagrostis*. If future phylogenetic work finds that they form a distinct clade, the old generic name of *Anomalotis* Steud., for which *Anomalotis quinqueseta* Steud. (syn. *Agrostis quinqueseta*) is the type species, could be used.

Unlike the typical subspecies, *Agrostis barbuligera* var. *longipilosa* has never been transferred to *Lachnagrostis*.

It is morphologically similar to *L. schlechteri*, with the lemmaawn attachment point being the major difference. However, the awn of *A. barbuligera* var. *longipilosa* is often adhered to the lemma back from the base to the mid-point, which can appear to be its attachment point. From the limited specimens examined (Appendix 1), *L. schlechteri* appears to have acute, rather than acuminate glumes, the lemma apices are not as drawn out into fine setae and the lemma hairs are dense and straight, to 0.5 mm long rather than being scattered and somewhat wavy, to 1 mm long, as for *A. barbuligera* var. *longipilosa*. Unlike *L. schlechteri* (Fig. 2b), examination of the lemma epidermis of *A. barbuligera* var. *longipilosa* shows that it, like var. *barbuligera* (Fig. 3a), also has a trichodium net pattern (Fig. 3b).

### ***Agrostis bergiana*, *A. aristulifera* and *A. subulifolia***

These three entities may represent the same taxon, but without a range of specimens to examine, such cannot be assessed at this time. Gibbs Russell et al. (1990), Clayton et al. (2006 onwards) and POSA (2009) recognised *Agrostis bergiana* and *A. subulifolia*, at least, as separate taxa. As for typical *Agrostis*, all three taxa lack a rachilla extension and at least *A. bergiana* and *A. aristulifera* have a lemma epidermis with a trichodium net (Fig. 1a; Björkman 1960). However, their palea to lemma length ratios are more akin to *Lachnagrostis* or *Polypogon*, and at least *A. bergiana* also displays a trichodium net on the palea.

Björkman (1960) notes that these taxa are similar to the *A. kilimandscharica* group from tropical Africa, except that most of the latter have strongly awned, pilose lemmas and a rachilla extension. The closest matches to *A. bergiana* from this group are *A. sclerophylla* and *A. pilgeriana* with which it shares the characters of a mid to upper dorsal lemma awn (rather than a basal awn), and a lack of a rachilla extension. Both *A. bergiana* and *A. sclerophylla* have glabrous lemmas. Further examination, and, more particularly, genetic assessment, may prove whether these grasses are part of the *A. kilimandscharica* group or not. What is clear from the current analysis is that they cannot be considered to belong to *Lachnagrostis*.

### ***Polypogon monspeliensis*, *P. strictus* and *P. tenuis***

These taxa have always been considered to be species of *Polypogon*, since *P. monspeliensis* was segregated from *Alopecurus* by Desfontaines (1798), by its awned glumes and lemma. The South African *P. strictus* and Ascension Island *P. tenuis* also have this feature. Björkman (1960) noted that both *P. monspeliensis* (Transcaspian, *Sintenis* 1773 (UPS)) and *P. tenuis* (South Africa, *Alcock* 6635 (S)) lack a trichodium net on their lemma epidermis. The current study confirms this feature for *P. monspeliensis* (Fig. 3e), at least.

Whether *P. strictus* and *P. tenuis* are the same taxon or not is beyond the scope of the current paper. Contemporary opinion (Goldblatt & Manning 2000; Raimondo et al. 2009) appears to be that they are not the same, and therefore any reference to *P. tenuis* in South Africa (e.g. Björkman 1960), should be applied to *P. strictus*.

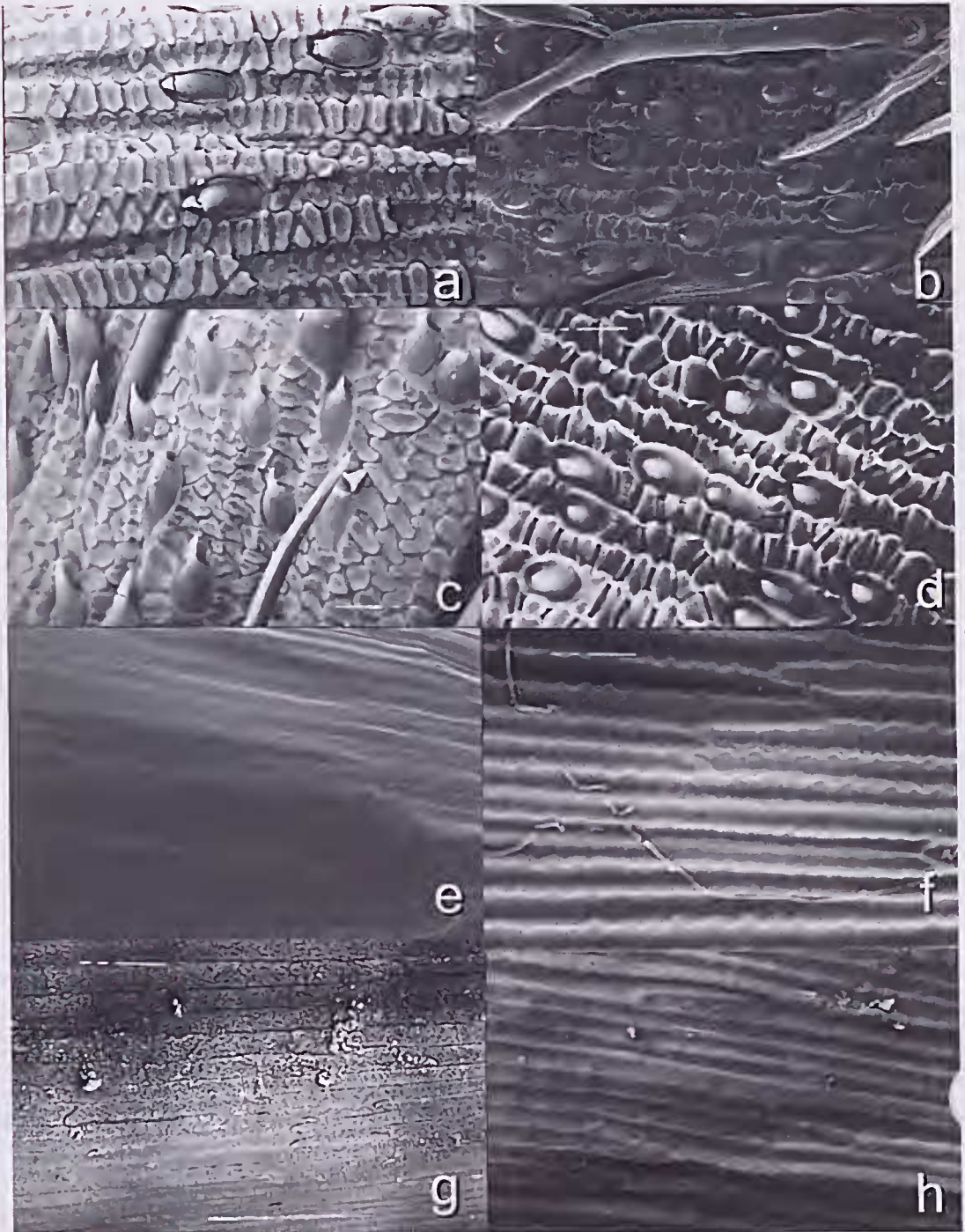
### ***Polypogon griquensis* (syn. *Agrostis griquensis*)**

This taxon was considered to be an *Agrostis* until 1990, because of its lack of awns on the glumes. The same is true of *Polypogon schimperiana* (Hochst. ex Steud.) Cope, a grass from tropical Africa, which was not recognised as a *Polypogon* until 1995. Cope (1995) noted that a stipitate spikelet falling whole from the pedicel (or part of the pedicel) was a more defining character for *Polypogon* than the presence of awned glumes. The current study shows the lemma epidermis of both *P. schimperiana* (Fig. 3f) and *P. griquensis* (Fig. 3g) without a trichodium net pattern and confirms that they do not belong to typical *Agrostis*.

### ***Polypogon viridis* (syn. *Agrostis verticillata*)**

The placement of the cosmopolitan *Agrostis verticillata* (syn. *A. viridis* Gouan, *A. semiverticillata* (Forssk.) C.Ch.) has always been problematic. Although the taxon has generally been recognised in the modern era as having spikelets that disarticulate below the glumes and therefore *Polypogon*-like, its lack of terminally awned glumes has kept it in *Agrostis* (as *A. semiverticillata*) in a number of floras e.g. Hitchcock (1951), Hubbard (1968), Rotar (1968), Willis (1970), Hitchcock and Cronquist (1973), Gould (1975), Barkley (1986) or as *A. viridis* in





**Figure 3.** Scanning Electron Microscope images (x1800) of the lower lemma epidermis of *Agrostis* taxa from South and East Africa and *Palypagon* taxa: **a.** *A. barbuligera* var. *barbuligera* (syn. *L. barbuligera*) (SJi); **b.** *A. barbuligera* var. *langipilasa* (SJi); **c.** *A. burttii* (syn. *A. kilimandscharica*) (SJi); **d.** *A. trachyphylla* (SJi); **e.** *Palypagon manspeliensis* (SJiii); **f.** *A. schimperiana* (syn. *P. schimperiana*) (SJii); **g.** *A. griquensis* (syn. *P. griquensis*) (SJiii); **h.** *A. verticillatus* (syn. *P. viridis*) (SJii). See Table 3 for voucher information; SJ = Jacobs pattern classification.

Jacobs (2009). Floras that listed the taxon as *Polypogon semiverticillatus* include Correa (1978) and Tsevelv (1984), and as *P. viridis* include Jessop and Toelken (1986), Gibbs Russell et al. (1990), Walsh and Entwisle (1994), Sell and Murrell (1996) and Edgar and Connor (2000). In the current study, the lack of a trichodium net on the lemma epidermis (Fig. 3h) confirms the taxon's placement in *Polypogon*, rather than in *Agrostis*.

## Taxonomy

Three South African *Agrostis* taxa are transferred to *Lachnagrostis* and new combinations made. Without having ready access to the range of type specimens, lectotypification of these names has not been attempted.

### *Lachnagrostis eriantha* (Hack.) A.J. Br., **comb. nov.**

*Agrostis eriantha* Hack. *Vierteljahrsschr. Naturf. Ges. Zürich* 49: 172 (1904).

**Types:** SOUTH AFRICA. Pretoria, Gauteng Province, *R. Schlechter* 4144, 6.i.1894 (syntype: W19160036234; isosyntypes: BM000922815, FR0030125, K000367406, MPU027097, PRE0592110-0, US00156418 (Cat. No. 75384), Z000073069); Middleburg, Eastern Cape, *R. Schlechter* 4052, 22.xii.1893 (syntype: W19050007172; isosyntype: BM000922816, K000367405, US01164502 (Cat. No. 3449125), Z000073070).

*Agrostis eriantha* var. *planifolia* Gooss. & Papendorf. *S. African J. Sci.* 181 (1945). **Type:** SOUTH AFRICA. Irene, Doornkloof, Transvaal, *Pole-Evans* 666, 3.xii.1922 (holotype: PRE0038905-0).

*Agrostis suavis* (Stapf.), *Bull. Misc. Inform. Kew* 1908: 227 (1908). **Type:** SOUTH AFRICA. Van Reenen, Natal, Wood 8913, 29.i.1903 (K000367407, K000367408, K000367409, NH0009346-0, NH0009975-0, W19160037226).

**Examined specimens:** see Appendix 1.

**Note:** One examined collection (*Davidson* 33256 & *Mogg* PRE38890) has completely glabrous lemmas (except for the callus). Otherwise it seems to conform to *Lachnagrostis eriantha*. Wood (1908) describes *L. suavis* as having lemmas 'laxly clothed with fine hairs on the back' but surprisingly his illustration (Plate 497) appears to have glabrous lemmas. In addition, the lemma awns in his illustration appear about 1–1.5× as long as the

lemmas, whereas the original description indicates awns 1.5–1.7× lemma length.

### *Lachnagrostis polypogonoides* (Stapf) A.J.Br., **comb. nov.**

*Agrostis polypogonoides* Stapf. *Fl. Cap. (Harvey)* 7: 549 (1900).

**Type:** SOUTH AFRICA. Muizenburg Vlei, Western Cape, *Wolley Dod* 2349, 9.i.1897 & ii.1897 (BM000922820, BOL139282, BOL139283, BOL139284, K000367375).

**Examined specimens:** see Appendix 1.

**Note:** *Polypogon polypogonoides* (Stapf) Forsan is not a validly published name: 'Forsan' being Latin for 'perhaps' and presumably intended as a comment on the identity of the specimen rather than as an authority of a new combination (Vorontsova & Simon 2012).

### *Lachnagrostis huttoniae* (Hack.) A.J.Br., **comb. nov.**

*Calamagrostis huttoniae* Hack. *Rec. Albany Mus.* 1(S): 340 (1905); *Agrostis huttoniae* (Hack.) C.E.Hubb. ex Gooss. & Papendorf. *S. African J. Sci.* 41: 179 (1945).

**Type:** SOUTH AFRICA. Shafton, Howick, Natal, 17.xii.1901, *H. Hutton* 384 (holotype: W19160037833; isotypes: BOL139281, GRA0000153-0, K000367395, US00157149 (Cat. No. 75386), W19160036845).

**Note:** No specimens of this taxon have been examined but the published descriptions suggest sufficient differences to maintain it as a separate species from *Lachnagrostis lachnantha*. Closer study may show otherwise.

*Agrostis lachnantha* var. *glabra* Gooss. & Papendorf was regarded by Gibbs Russell et al. (1990) as 'not distinct'. For the same species, Victor et al. (2012) noted that 'hairs on the lemma are variable in length and cannot reliably be used to distinguish varieties'. Victor et al. (2012) also regarded callus hair length, used to distinguish *A. eriantha* var. *planifolia* Gooss. & Papendorf, as 'not a reliable character'. Because of the uncertainties related to the distinctiveness of these varieties, they have not been transferred to *Lachnagrostis* at this time. The variation observed for a number of South African *Lachnagrostis* in the current study suggest that further fieldwork and examination of a wider range of material is required and may facilitate the recognition or reduction of additional taxa in the future.



## Conclusions

The native South African Agrostidinae segregate into four distinct morphological groupings:

1. *Agrostis natalensis* and/or *A. continuata* – contracted panicle with fasciculated branches, spikelet disarticulation above the glumes, short palea relative to lemma, glabrous to near glabrous lemma, trichodium net present on lemma epidermis, with or without rachilla extension.
2. *Agrostis barbuligera* and *A. bergiana* (probably incl. *A. subulifolia*) (with strong affinities to the *A. kilimandscharica* / *A. mannii* group of tropical montane Africa) – open to loosely contracted panicle, spikelet disarticulation above the glumes, long palea relative to lemma, hairy or glabrous lemma, trichodium net present on lemma epidermis, with or without rachilla extension.
3. *Lachnagrostis lachnantha*, *L. huttoniae*, *L. schlechteri*, *L. eriantha* and/or *L. suavis* and *L. polypogonoides* – open to loosely contracted panicle, spikelet disarticulation above the glumes, long palea relative to lemma, usually hairy lemma (glabrous in *L. huttoniae*), trichodium net absent on lemma epidermis, with or without rachilla extension.
4. *Polypogon strictus* and *P. griquensis* – spiciform to densely contracted panicle, spikelet disarticulation below the glumes, long palea relative to lemma, glabrous lemma, trichodium net absent on lemma epidermis, without rachilla extension.

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## Appendix 1: Specimens of *Polypogon* (MEL), *Agrostis* (MEL, PRE) and *Lachnagrostis* (AK, CHR) examined for comparison with published descriptions

### *Polypogon monspeliensis*

**SOUTH AFRICA.** In ausgetrocknete Walleien (sumpfartige Stelle) an Zwartkopsrivier (i.e. Blackcap River) 1:e Höhe (Distr. Uitenhage), xii.1829, [C.F. Ecklon] 1828 (as 854 *Setaria* [U. J.] No.969) [probably equivalent to *P. polysetus* Steud.] (MEL2386787); J.F. Drège a, ex hrb Sonder (as *P. strictus* (*P. monspeliensis* var. *pallens*)) [Isosyntype of *P. monspeliensis* var. *pallens* Nees from Olifanttrivier fluvium (i.e. Elephant River Valley) near Ebenezar (Nees von Esenbeck 1841b)] (MEL2386783); near Grahamstown [Grand Kraal (Stapf 1900)], *P. MacOwan* 1281 (MEL2386788). **AUSTRALIA.** Fish Creek Rail Station, Victoria, 5.xii.1994, *A. Paget* 1148 (MEL2026751) [SEM image].

### *Polypogon strictus*

**SOUTH AFRICA.** 2–11 [Uitenhage, Zwartkopsrivier, Villa Paul Maré to Uitenhage – November (Gunn & Codd 1981)], [C.F. Ecklon & K.L.P. Zeyher in part] taxon 59, ex hrb Sonder [probably *P. strictus* var. *major* Nees] (MEL2386786, MEL2386789); 78 [Cape Doornhogde (Gunn & Codd 1981)], [C.F. Ecklon & K.L.P. Zeyher], ex hrb Sonder [probably *P. strictus* var. *minor* Nees] (MEL2386784); J.F. Drège, ex hrb Sonder (as *P. strictus* var. *spelaeus*) [Isotype of *P. strictus* var. *spelaeus* Nees from a cave on the Witt 8ergen at 6000' with *Podosemum lachnanthum* var. *humile*, Tulbagh, Western Cape (Nees von Esenbeck 1841b)] (MEL2386785); Chapman's Peak, Cape Peninsula, xii.1919, *H. Andreae* 114 (as *P. tenuis* ex PRE) (MEL2386782).

**Notes:** Most of the specimens of *Polypogon* above have no clear collector and location information, but examination of the literature has enabled these details to be identified. The three specimens of *P. strictus* ex hrb Sonder (MEL2386786, MEL2386784, MEL2386785) were found in the same folder at MEL, along with the specimen of *P. monspeliensis* ex hrb Sonder (MEL2386783). It seems that the earliest plant collectors in South Africa (Zeyher 1822–1842, Ecklon 1823–1828, Drège 1826–1834) initially considered any indigenous *Polypogon* population to be of *P. strictus* Nees, rather than of the European *P. monspeliensis* Desf., as *P. strictus* often appears on their collection sheets of the latter taxon. Nees von Esenbeck (1841b) described three varieties of *P. monspeliensis*: 'α Maior' syn. *P. polysetus*

Steud., 'β Minor' syn. *P. monspeliensis* var. *capensis* Steud. and 'γ Pallens', and three varieties of *P. strictus*: 'α Maior', 'β Minor' and 'γ Spelaeus' for South Africa. Although only the one MEL specimen of *P. strictus* has a varietal name attached (i.e. var. *spelaeus*), the other two specimens conform to the descriptions of var. *major* and var. *minor*.

Steudel (1829) used the numbers 968 and 969 to designate *P. monspeliensis* and *P. polysetus*, respectively. These taxon numbers appear to be the same as used by the Unio Itineraria (U. J.), a botanical exchange club, founded and managed by E.G. Steudel and C.F. Hochstetter (Gunn & Codd 1981). For example, the label of the type of *P. polysetus* (S14-34076 image seen) notes 'U. J. Ecklon' and the number '969' but bears the location 'An feuchten Stellen der 2:e Höhe des Löwenberges (i.e. Lion Mountains)'. Steudel (1829) described the type location as 'In paludosis altitudinis 2 montis dorsei leonis'. A duplicate of MEL2386787 (including the same label details) is also at S (S14-34067 n.v.). The number '854' for *Setaria* appears to be a taxon number which was mistakenly applied to MEL2386787, probably as an original label, due to the superficial likeness of the panicles of *Setaria* and *Polypogon* in the field. Steudel (1829) also noted '*Setaria*' for collections of *P. monspeliensis* and *P. polysetus*, presumably describing original label inscriptions.

The numbers 2–11 (or 2.11) and 78 are codes for Ecklon and Zeyher's collection localities (Gunn & Codd 1981): the 11 referring to the month of sampling. An identical *P. strictus* label to MEL2386789 bearing the number 59 and the locality – month code 2.11 is attached to the Missouri Botanical Garden Herbarium sheet (MO-2397264 image seen), even though the specimen has been since determined as *P. monspeliensis*. As the number 60 and the locality code 85 [eastern side of Table Mountain at Constantia (Gunn & Codd 1981)] is associated with a label on a further South African specimen of *P. monspeliensis* at MO (MO-2397263 image seen), it appears that the numbers 59 and 60 are also taxon numbers (separate to those of Steudel 1829 and Ecklon & Zeyher 1834), rather than collection numbers or location codes.

### *Agrostis griquensis* (syn. *Polypogon griquensis*)

**SOUTH AFRICA.** Bloemfontein, near Tempe farm, Free State, 6.x.1917, Geo. Potts 2467 (MEL2386781) [NSW duplicate imaged by SEM – see Table 3].



***Agrostis semiverticillata* (syn. *Polypogon viridis*)**

**SOUTH AFRICA.** Umbilo River, Durban, KwaZulu-Natal, C.J. Word 5948 (MEL2386779); Erigaro, British Somaliland, 29.v.1939, A.S. McKinnon s.n. (MEL2386780).

***Agrostis bergiana***

**SOUTH AFRICA.** Table Mountain, Western Cape, December, C.F. Ecklon (as 943) ex hrb. Sonder (MEL2386774) [Isotype of *A. ecklonis* Trin. typified by L. Pignotti (W) 2010].

**Note:** A number of authorities (e.g. Tropicos 2015; JSTOR 2015) note 943 as Ecklon & Zeyher's collection number for *Celastrus heterophyllus* Eckl. & Zeyh. when in fact, Ecklon and Zeyher (1834) list it as the taxon number for this species. However, 943 was also used to designate *A. capensis* Steud. (syn. *A. bergiana*) in the distribution of specimens by the Unio Itineraria. Steudel (1829) appears to have mistakenly listed the taxon number for *A. capensis* as 493 (when all the surrounding grass taxon numbers are in the 900s).

***Agrostis continuata***

**SWAZILAND.** Near Mbabane: valley of Black Mbuluzi River, i.1965, K.D. Gordon-Groy 65/102 (MEL2323539).

***Agrostis barbuligera* var. *barbuligera* (syn. *Lachnagrostis barbuligera* var. *barbuligera*)**

**SOUTH AFRICA.** Holmes Farm, portion Vredesrus, NNE of Maclear, North-eastern Cape, 31.x.1994, S.P. Bester 3074 (PRE835477); Estcourt, KwaZulu-Natal, 21.xi.1940, *Curator Pretorio* E909 (PRE38936). **LESOTHO.** Top of Organ Pipes Pass, Cathedral Peak, 26.i.1978, L. Smook 1081A (PRE513672); Reed's Camp, Tschlangana Valley, Basutoland, 8.i.1960, *Jocot-Guillormod* 3737 (PRE40497) [SEM image]; Schlabathebe National Park, Ntloana-Tsoana, 13.xii.1977, F.K. Hoener 1907 (MEL2323525).

***Agrostis barbuligera* var. *longipilosa***

**SOUTH AFRICA.** Bethlehem, Free State, 24.i.1965, B.R. Roberts 3280 (PRE38919) [SEM image]; Steenkampsberge, Mpumalanga, 7.xii.1983, L. Smook 4826A (PRE670162); 14 km van Sabie na Graskop, Mpumalanga, 24.x.1988, J. Sooymon 76 (as *Agrostis lachnantha*) (PRE742515). **SWAZILAND.** Forbes Reef Road, Mbabane, 1.xi.1957, R.H. Compton 27192 (PRE38923); Lydenberg na Sabie, Mpumalanga, 24.x.1988, J. Soayman 57 (PRE742618); Pilgrims Rest, Mpumalanga, 15.xii.1975, P.C.V. Du Toit 1071 (PRE356993); Wakkerstroom, Free State, 20.xi.1962, N.J. Devenish 951 (PRE104231).

***Agrostis eriantha***

**SOUTH AFRICA.** Tafelkop, Wakkerstroom, Oshoek, Free State, 1982, N.J. Devenish 3843 (PRE664945) [SEM image]; Bethlehem, Free State, 1.i.1963, L.C.C. Liebenberg 7017 (PRE40503); New Scotland Special, Athole, P.R. Station, Ermelo, Mpumalanga, 10.ii.1943, L.E.W. Codd 392 (PRE38909); Athole Pasture Research Station, Mpumalanga, 11.i.1936, C.M. Norval 122 (PRE38897); Crown Mines Marsh, Johannesburg, 11.iii.1965, L. Dovidson 33256 & A.O.D. Mogg (PRE38890).

***Agrostis avenacea* (syn. *Lachnagrostis filiformis*)**

**SOUTH AFRICA.** McGregor, Riviersonderendberge, Western Cape, 16.x.1988, J.J. Spies 3922 (PRE742585); Barrydale, Tradouw Pass, Western Cape, 13.x.1981, L. Smook 3756 (PRE608795); Emberton Farm, Knysna, Western Cape, 24.xi.1980, A.O. Crook 2334 (PRE610390); Graskop na Bosbokrand, Northern Province, 24.x.1988, J. Sooymon 78 (PRE742615).

***Agrostis lachnantha* (syn. *Lachnagrostis lachnantha*)**

**SOUTH AFRICA.** NW of Olifantshoek in Langeberge, Western Cape, 10.viii.2000, L. Smook 10950 (PRE588744); Langs Modderrivier Glen, Bloemfontein, Natal, 31.i.1986, J.J. Spies 2662 (PRE671808); Cathedral Peak Park, Baboon Rock, KwaZulu-Natal, 21.xii.1988, H. Du Plessis 99 (PRE741413); Anne's Hoek, Buffelskloof Nature Reserve, Lydenberg, Mpumalanga, 10.xii.2004, J.E. Burrows 8673 (PRE770789); Monte Boschberg, Western Cape, P. MocOwan 1667 ex hrb Sonder, (MEL2371711); J.F. Drège o, ex hrb Sonder (as *Podosomeum lochnanthum* var. *humile* Nees), (MEL2371712); Willow Grange, KwaZulu-Natal, x.1905, J. Medley Wood 9942 ex hrb Natal (MEL2386776); Rooidraai farm, Lydenburg, Mpumalanga, 7.xii.1935, L.C.C. Liebenberg 3491 ex PRE (MEL2386777); 1.12 [Worcester, Waterfall, 1-2000', December (Gunn & Codd 1981)] [C.F. Ecklon & K.L.P. Zeyher], taxon 61 [isosyntype of *Podosomeum lochnanthum* Nees (Nees von Esenbeck 1841b)] (MEL2386778); *unknown*, ex hrb Sonder (as *Agrostis neesii* (*Podosomeum* [*Podosomeum*] *ongustum* Nees)) (MEL2386775).

**Note:** Some of the early specimens at MEL have few details attached. However, a search of the literature has managed to locate much of the missing data. See notes under *Polypogon strictus* above for explanations of locality codes and taxon numbers.

***Agrostis polypogonoides***

**SOUTH AFRICA.** Lokenberg, Northern Cape, 24.i.1954, Acocks 17580 (PRE40478); Villiersdorp, Western Cape, 8.i.1896, R. Schlechter 3797 (PRE38861).

***Agrostis schlechteri* (*Lachnagrostis schlechteri*)**

**SOUTH AFRICA.** Suurvlakte, Paarl, South-west Cape, 9.ii.1947, *E.E. Esterhuysen* 13727 (PRE40537); Stellenbach, Cape Province, xii-i.1947, *L. Visser* PRE35059 (PRE40540).

***Lachnagrostis leptostachys***

**NEW ZEALAND.** Antipodes Is., 8.i.1909, *unknown* (CHR333324); De La Vire, Campbell Is., 7.i.1961, *Zorov s.n.* (CHR119513).

***Lachnagrostis lyallii***

**NEW ZEALAND.** Wapiti Lake, 12.iii.1985, *Platt s.n.* (CHR521641); cult. ex Tongariro National Park, 3.iii.1971, *P.J. de Lange* 5203 (AK252979).

***Lachnagrostis pilosa* subsp. *pilosa***

**NEW ZEALAND.** Isolation Ck., Waima River, xii.1979, *Druce s.n.* (CHR363565); Cape Palliser, Wairarapa, xii.1973, *Druce s.n.* (CHR273108); Lake Wakatipu, xii.1991, *Druce s.n.* (CHR475873); Bold Peak, *Simpson s.n.* (CHR370168).

***Lachnagrostis striata*:**

**NEW ZEALAND.** Kaweka Lakes, xii.1964, *Druce s.n.* (CHR131763); Makinkiri Tarus, ii.1981, *Druce s.n.* (CHR389436).